THE TAXONOMY AND MORPHOLOGY OF MACRANTHERA FLAMMEA (OROBANCHACEAE)

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ABSTRACT

Macranthera flammea (Bartr.) Pennell is a rare, biennial species endemic to the pine flatwoods of the lower coastal plain of the southeastern United States. Field, experimental garden, and herbarium studies were used to update the species description. The taxonomic history of the species is reviewed. Recognition of more than one taxon in the genus is not warranted because differences in calyx length and lobing are due to the placement of flower units within the architecture of the inflorescence on individual plants. A map of the species' range is provided.

RESUMEN

Macranthera flammea (Bartr.) Pennell es una especie rara, bienal endémica de los pinares de la llanura costera inferior del sudeste de los Estados Unidos. Se hicieron estudios de campo, jardín experimental, y herbario para poner al día la descripción de la especie. Se revisa la historia taxonómica de la especie. No se necesita reconocer más de un taxon en el género ya que las diferencias en la longitud del cáliz y lobulación se deben a la colocación de las unidades florales en la arquitectura de la inflorescencia en los distintos individuos. Se aporta un mapa del área de las especies.

INTRODUCTION

Macranthera is monotypic; the single species *M. flammea* is endemic to the southeastern coastal plain of the United States and is commonly referred to as "flame flower" or "hummingbird flower." It is listed as endangered by the state of Florida (Coile 2000). The genus was formerly placed in the Scrophulariaceae, but recent studies have shown that family to be a heterogenous group (Olmstead et al. 2001); the hemiparasitic taxa are better placed in the Orobanchaceae.

Here, an updated species description and range map are provided. More detail on the life history and pollination biology is documented by Alford (2000).

NOMENCLATURAL HISTORY

The many names that have been proposed for this species indicate the difficulty that early botanists had in understanding the taxon and its generic placement (Table 1). William Bartram (1791) first described *M. flammea* as *Gerardia flammea* during his travels through the southeastern states during 1773–1777.

In 1834, after examining an unlabeled specimen in the herbarium of the Academy of Natural Sciences, Philadelphia (PH), Nuttall published the genus

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Table 1. Synonyms for Macranthera flammea.

Synonym	Year		
Gerardia flammea W. Bartram	1791		
Conradia fuchsioides Nutt.	1834		
Macranthera fuchsioides (Nutt.) Benth.	1836		
Macranthera lecontei Torr.	1837		
Russelia flammea (Bartr.) Raf.	1837		
Flamaria coccinea Raf.	1837		
Toxopus gymnanthes Raf.	1837		
Toxopus calycinus Raf.	1837		
Tomilix bracteata Raf.	1837		
Dasystoma tubulosa Bertol.	1853		
Macranthera fuchsioides var. lecontei (Torr.) Chapman	1860		
Conradia lecontei (Torr.) Kuntze	1891		
Macranthera flammea (Bartr.) Pennell	1913		

Conradia as a dedication to the late Solomon W. Conrad, a Professor of Botany at the University of Pennsylvania. Nuttall proposed the name Conradia fuchsioides, because "the corolla and long exerted stamens put one in mind of some gigantic Fuchsia" (Nuttall 1834).

Bentham (1835) applied the name *Macranthera fuchsioides* (Nutt.) Benth., because *Conradia* had been previously applied to a genus of Gesneriaceae by Martius. The name *Macranthera* means "long anther." Bentham and LeConte were both originally cited as authors for the genus (Hooker 1835), although Bentham (1835) felt that Torrey alone should receive credit for the generic name.

Torrey (1837) described a second species, *M. lecontei* (sometimes spelled *lecontii*), from a specimen collected in Georgia in 1831 by LeConte. He believed it was distinct because the segments of the calyx were entire, linear-lanceolate, and approximately one-third the length of the corolla. In *M. fuchsioides* the segments of the calyx are dentately lobed and often as long as the corolla tube [on LeConte's specimen (NY), Torrey applied the name Conradia *lecontei* Torr., along with a note stating the segments of the calyx are entire]. The specimen itself is damaged, but an attached illustration depicts the entire sepals. Torrey actually published the species (1837) not as *C. lecontei*, but as *M. lecontei*, since Bentham (1835) had determined that *Conradia* was already in use.

Pennell (1935) questioned the authenticity of the collection site of *M. lecontei*, which was purportedly along the Altamaha River in Liberty County, Georgia, because that site was far removed from other known occurrences of the species. However, the species has been observed along the Altamaha River as recently as 1997 (M. Hopkins, pers. comm.).

Rafinesque (1837) proposed many new names for Macranthera (see Table 1).

Macranthera flammea Raf. was proposed on the basis of Bartram's original description.

However, Rafinesque thought the genus name *Macranthera* was inappropriate because he did not believe the anthers to be of considerable length, and he suggested the name *Toxopus*, meaning "incurved peduncles." He substituted *Toxopus gymnanthes* Raf. for *M. lecontei* Torr. and *Toxopus calycinus* Raf. for *M. fuchsioides* (Nutt.) Benth. He further proposed the genus *Tomilix* meaning "cut calyx" for *M. fuchsioides*, suggesting that this species be treated as either a subgenus or new genus because of the condition of the calyx and the presence of what he felt to be a bifid style. He proposed the binomial *Tomilix bracteata* Raf. as an additional name for *M. fuchsioides* (Nutt.) Benth. The new genus *Flamaria*, as in *Flamaria coccinea* Raf., was also proposed

Bertoloni (1853) described a new genus and species, *Dasystoma tubulosa*, after examination of collections in GH, NY, and PH. Chapman (1860) treated *M. lecontei* as a variety of *M. fuchsioides*, and Kuntze (1891) resurrected the genus *Conradia* on the basis of the type specimen that Torrey had originally identified as *C. lecontei*.

Pennell (1913) combined the two species of *Macranthera* into one, writing: "this difference [in the calyx] is due wholly to age of the flower, as may be readily seen in the field; young flowers are as in *lecontei*, while with age the sepals continue growing and become lobed while the corolla shrivels and shortens in situ, so bringing about the *fuchsioides* state." Pennell suggested that, because Bartram originally described the species, the accepted name must become *Macranthera flammea* (Bartr.) Pennell. He argued that Bartram named his species for its "flame-coloured" flowers which is a fitting description. *Gerardia* was rejected as a generic name because it is a synonym for *Agalinis*.

Later, many were concerned about the validity of Bartram's binomials (Fernald 1944; Rickett 1944; Merrill 1945). Rickett (1944) argued that Bartram's binomials are inappropriate because they appear in a publication that is not always consistent with the Linnean system of binomial nomenclature. Merrill (1945) defended Bartram's binomials, writing: "the proportion of binomials to polynomials, 358 to 2, is too great in favor of the former to justify the elimination of Bartram's work." Wilbur (1971) argued that, if a Bartram binomial is accompanied by an adequate description, the publication of the binomial should be considered valid.

Additional controversy surrounds Bartram's description of his collection site. He probably confused the locality of his specimen of *Macranthera* with that of the mint *Calamintha coccinea* (Nutt.) Benth. While traveling along the Tensaw River near "Taensa" (near or in Baldwin Co, Alabama), Bartram (1791) recounts the following observations: "These stony gravelly heights produce a variety of herbaceous plants, but one in particular I shall mention on account

of its singular beauty. I believe it is a species of *Gerardia (Gerardia flammea)*; it grows erect, a single stem from a root, three or four feet in height, branching very regularly from about one half its length upwards, forming a cone or pyramid, profusely garnished with large tubular labiated scarlet or flame coloured flowers, which give the plant a very splendid appearance even at a great distance." This description closely describes, for the most part, the form and appearance of *M. flammea*, but the locale and scarlet flower color are more appropriate for the mint *Calamintha coccinea* (Merrill 1945). Unlabeled specimens of both plants were found in Bartam's collection at the Natural History Museum in London (Pennell 1935). Bartram's description is applicable in part to both plants (Table 2), but Pennell (1935) believed Bartram's description to be most applicable to *M. flammea*.

SPECIES DESCRIPTION

Macranthera flammea is generally an herbaceous biennial of the Orobanchaceae Rosette leaves on juvenile plants are oblanceolate to spatulate. Leaves are glabrous with entire or pinnately lobed margins, depending on developmental stage. Rosettes are variable in leaf number and leaf size, having 3–46 leaves per rosette with lengths of 3–33 cm and widths of 0.8–3.6 cm (Fig. 1).

Plants may be more appropriately classified as monocarpic perennials because they may remain in the rosette phase for more than one year. Rosettes that have attained a critical size are triggered to reproductive states by an increase in day length. Before a rosette bolts into a flowering adult, it begins to produce pinnately lobed leaves.

Reproductive plants of *M. flammea* are mostly 15–30 dm tall, with stems that are obtusely four-angled and essentially nonbranching below the candelabralike spreading inflorescence. Cauline leaves are opposite and sessile or have short, winged petioles. Lower leaves are 8.5–16 cm long and 2–6 cm wide, lanceolate to ovate, and pinnately lobed. Leaves are progressively reduced upward along the stem; the uppermost are 4–7 cm long and 1–2.5 cm wide, slightly lobed, and toothed or entire. Blades are glabrous, or with minutely ciliate margins. Rosettee and lower leaves are usually shed by the time of anthesis.

The paniculate inflorescence contains long, indeterminate, racemose branches (Fig. 2). Flowers are axillary to a reduced, usually entire, foliar bract (see illustration in Godfrey and Wooten 1981). Pedicels are 1–2 cm long, becoming reflexed in fruit. The calyx is fused with five short lobes that are equal and linear and 7.5–15 mm long. The corolla is bright orange, fleshy, 2–2.5 cm long, short pubescent without, and glabrous or slightly pubescent at the base within. A whitish nectar chamber at the corolla base is 4 mm long.

The corolla turns brown to black with age. The tube is cylindrical and much longer (20-23 mm) than the two-lipped lobes (3-4.5 mm), with an adaxial lip

TABLE 2. Similarities (of Bartram's description	of Macranthera and Calamintha.
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	Macranthera	Calamintha	
Habitat	wet boggy thickets	stony gravelly heights	
Plant branching	regular, in upper half	intricately, from base	
Plant shape	tall pyramidal cone	low spreading	
Plant height	3-8 feet	3–4 feet	
Corolla shape	tubular labiated	tubular labiated	
Corolla color	flame colored	scarlet	

that is two-lobed and erect and a three-lobed, spreading abaxial lip. The four contiguous stamens are equal in length and exerted. The filaments are orange and become about twice as long as the corolla tube, up to 46 mm. The ovary is ovoid and has a slender style that is to 46 mm and a linear-clavate stigma. Mature bicarpellate capsules are 9.5–13 mm long, 7.5–10.5 mm wide, loculicidal, and slightly pubescent. The seeds are brownish black, 2.5–3 mm long, half as wide, irregular in shape (angular-lunate to triangular) with two or three fluted membranous wings. Specimens of *M. flammea* become black upon drying (due to presence of orobanchin or iridoid compounds as in related parasitic taxa).

The species description is verified by examination of collections (Appendix 1) from major and regional herbaria: Angus K. Gholson (personal collection designated AKG; it will eventually become part of FLAS), University of Florida (FLAS), Florida State University (FSU), Gray Herbarium (GH), University of Southern Mississippi (no official abbreviation, designated HATT here for convenience), Jacksonville State University (JSU), Louisiana State University (LSU), Missouri Botanical Garden (MO), New York Botanical Garden (NY), Old Dominion University (OD), Academy of Natural Sciences of Philadelphia (PH), Smithsonian Institution (US), University of Georgia (GA), University of Mississippi (MISS), University of South Alabama (USAM), Valdosta State University (VSC), and Vanderbilt University (VDB).

The species description is also supplemented by measurements taken from several plants at two field sites: Thomas Co., Georgia, at Greenwood or GWD (*Alford 1077* at FSU) and Liberty Co., Florida, in the Apalachicola National Forest or ANF (*Alford 1064* at FSU).

Range and Habitat.—The range of *M. flammea* (Fig. 3) extends along the lower coastal plain from Georgia to southeast Louisiana. This species requires mesic habitats of bogs and thickets and is ecotonal, occurring in the sandy acid soils of pine flatwoods along the margins of seepage slopes and shrub-tree bogs or bays (Small 1933). It can occasionally be found in shallow water of cypressgum ponds or depressions (Godfrey & Wooten 1981). It does not tolerate standing water and can only be found in areas where water flow is sufficient (Determann et al. 1997).

Macranthera flammea



Fig. 1. Macranthera flammea. a, lower cauline leaf; b, branch of inflorescence; c, flower with exserted stamens and style; d, fruit with persistent style. Modified from drawing by Jean C. Putnam-Hancock in Chafin (2000); used by permission.

Woody plants associated with M. flammea include: Acer rubrum L., Aronia arbutifolia (L.) Ell., Clethra alnifolia var. tomentosa (Lam.) Michx., Cliftonia monophylla (Lam.) Britt. ex Sarg., Cyrilla racemiflora L., Fraxinus caroliniana Mill., Ilex coriacea (Pursh) Chapm., Ilex glabra (L.) Gray, Itea virginica L., Liriodendron tulipifera L., Lyonia lucida (Lam.) K. Koch, Magnolia virginiana L., Myrica cerifera L., Nyssa sylvatica var. biflora (Walt.) Sarg., Persea palustris

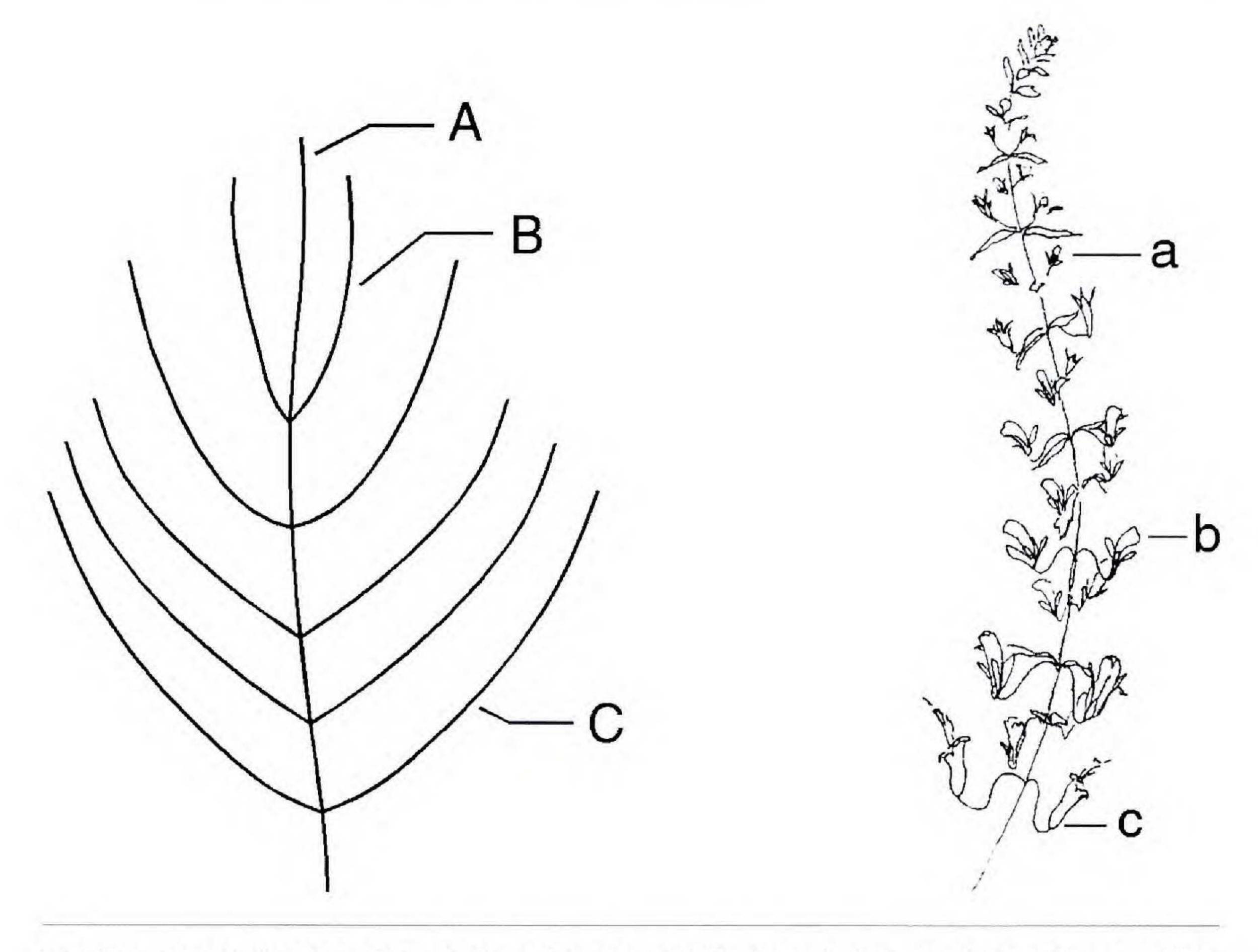


Fig. 2. Raceme and bud positions for study of morphological variability. A, terminal raceme of panicle; B, upper axillary raceme; C, lower axillary raceme; a, upper bud on branch; b, median bud; c, lower bud.

(Raf.) Sarg., Pinus elliottii Engelm., Pinus palustris Mill., Pinus serotina Michx., Rhododendron viscosum (L.) Torr., Viburnum nudum L. Herbaceous associated taxa include: Andropogon virginicus L., Aristida stricta Michx., Arnoglossum sulcatum (Fern.) H. Robins., Arundinaria gigantea (Walt.) Muhl., Coreopsis gladiata Walt., Elephantopus nudatus Gray, Erianthus giganteus (Walt.) Muhl., Eryngium integrifolium Walt., Helianthus angustifolius L., Hypericum cistifolium Lam., Hypericum galioides Lam., Hypericum tetrapetalum Lam., Hyptis alata (Raf.) Shinners, Juncus validus Coville, Ludwigia hirtella Raf., Osmunda cinnamomea L., Panicum scoparium Lam., and Pteridium aquilinum (L.) Kuhn.

Common Name.—This species is commonly referred to as flame flower or hummingbird flower. In at least one instance, it was referred to as Spanish princess (Pickens 1955). Flame flower is an appropriate name for *M. flammea*. It is representative of the specific epithet because of the flame-like appearance of the orange-yellow corolla (and the candelabra branching habit lends a flame shape to the inflorescence). Hummingbird flower is less desirable as is could be applied to any number of species that have red or orange tubular corollas.

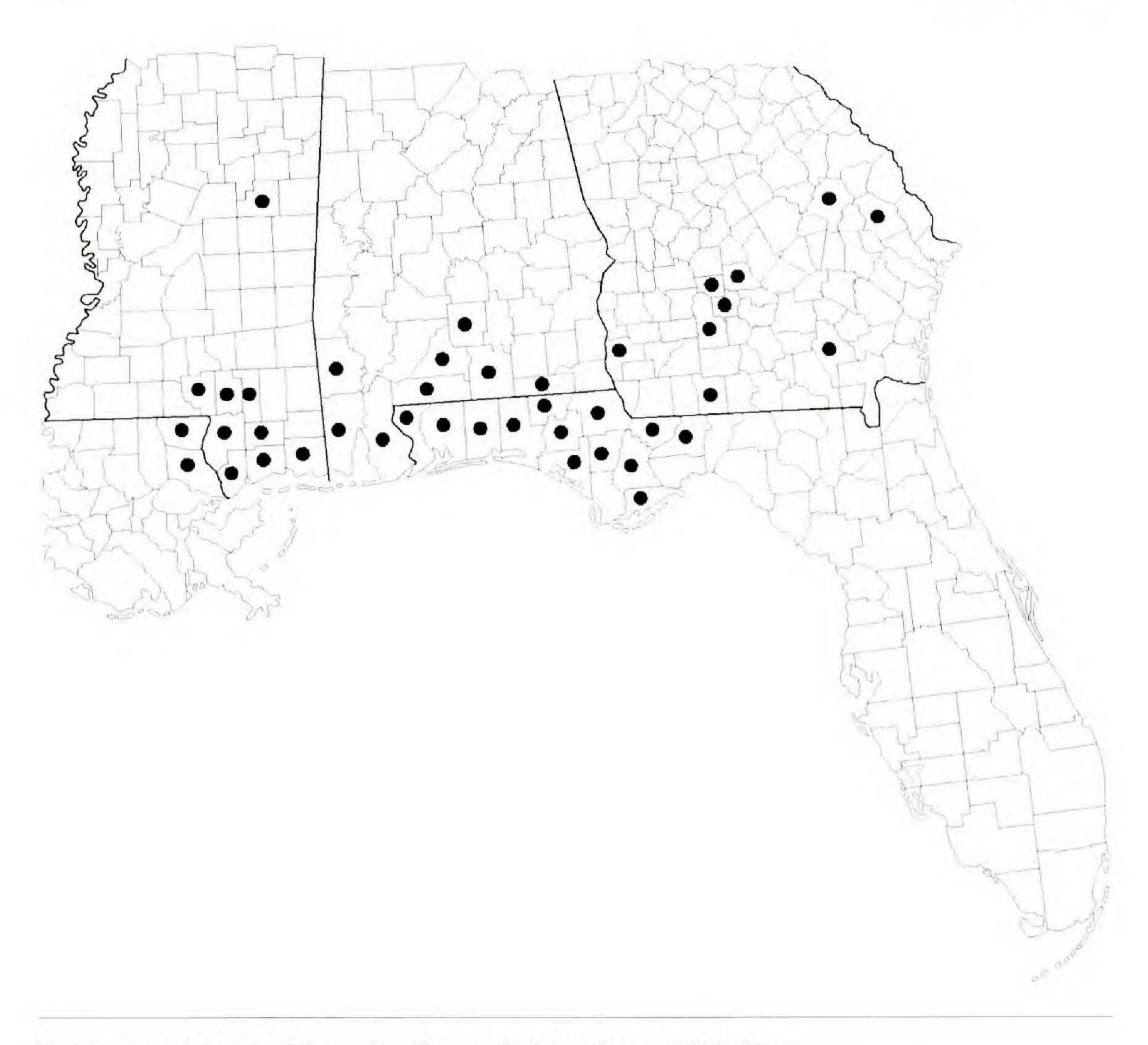


Fig. 3. Documented range of Macranthera flammea in the southeastern United States.

EXAMINATION OF MORPHOLOGICAL VARIABILITY

Taxonomists base plant descriptions on the morphology of repeating modular units of construction, i.e. leaves, flowers, etc. because, although the number of units and size of the whole plant can vary greatly with age and environmental conditions, genetic control maintains consistent size and form of modular units (Harper 1977). Differences between species depend on the morphological form of repeating units. Variation in characters may exist across the range of a species, within a single population, and even within a single individual.

Macranthera inflorescences are indeterminate as defined by Harper (1977). Meristems continue to produce new flowers and leaves, and the position of an individual flower on the inflorescence reflects its age. By measuring changes in floral characters through time, we determined how each individual flower is affected by its location within the architecture of an individual plant and whether Pennell (1913) was correct in stating that the differences (in calyx

length and lobing) between the two species recognized at that time (M. fuchsioides and M. lecontei) were in fact attributable to age.

We examined herbarium specimens (Appendix 1) to determine the extent of variability of morphological characters across the species' range. Characters considered were calyx length, corolla tube length, corolla lobe length, corolla width, pedicel length, bract length, fruit length, and fruit width. Because it was not always possible to know which part of the plant was represented by the herbarium specimen, we standardized measurements by choosing floral buds at the stage of development just prior to the separation of the corolla lobes. Lengths and width of mature fruits and, when available, the length and width of the lower and uppermost (just below the inflorescence) stem leaves were measured.

To examine the extent of variability within a population and also within a single plant, we randomly selected five plants from the established study site at GWD in Thomas Co., Georgia, that represented the range of environmental conditions for the site. Three flower buds (upper, median, and lower) were marked on each of three racemes of the inflorescence (terminal, upper axillary, and lower axillary), for a total of nine measured buds per plant (Fig. 4). Characters previously mentioned were then measured on marked buds every four days for a period of one month. We measured fruit and foliage on 12 plants randomly selected from the population.

Means and standard deviations were calculated for all measured characters from herbarium specimens (Table 3). Means and standard deviations of floral characters from the GWD sample population were calculated from characters measured on 28 August 1997 in order to determine the amount of variability for characters within the plant architecture at a given time (Table 3).

The standard deviations of measured characters (Table 3) for herbarium specimens reveal that although the floral tissue components (corolla tube) of the flower show little variability, variability is higher in the chlorophyll containing components (calyx, pedicel, and bract). The GWD population exhibited more variability overall in corolla tube and calyx lengths than the herbarium specimens because smaller and larger buds were included.

Plant 59 of the GWD sample population was selected to illustrate growth changes over time in corolla tube length (Fig. 4) and calyx length (Fig. 5) for each bud position of the three racemes examined. For each raceme, the corolla tube expanded rapidly (Fig. 4). On the terminal and lower axillary racemes, the tubes expanded to 22–24 mm before anthesis. Those of the upper axillary raceme reached only 20–22 mm. Corolla tube width was between 4 and 5 mm for all flowers examined.

The calyces of the lower and median buds on the terminal raceme (Fig. 5, a) had nearly reached their limits of expansion at the initial measuring, but

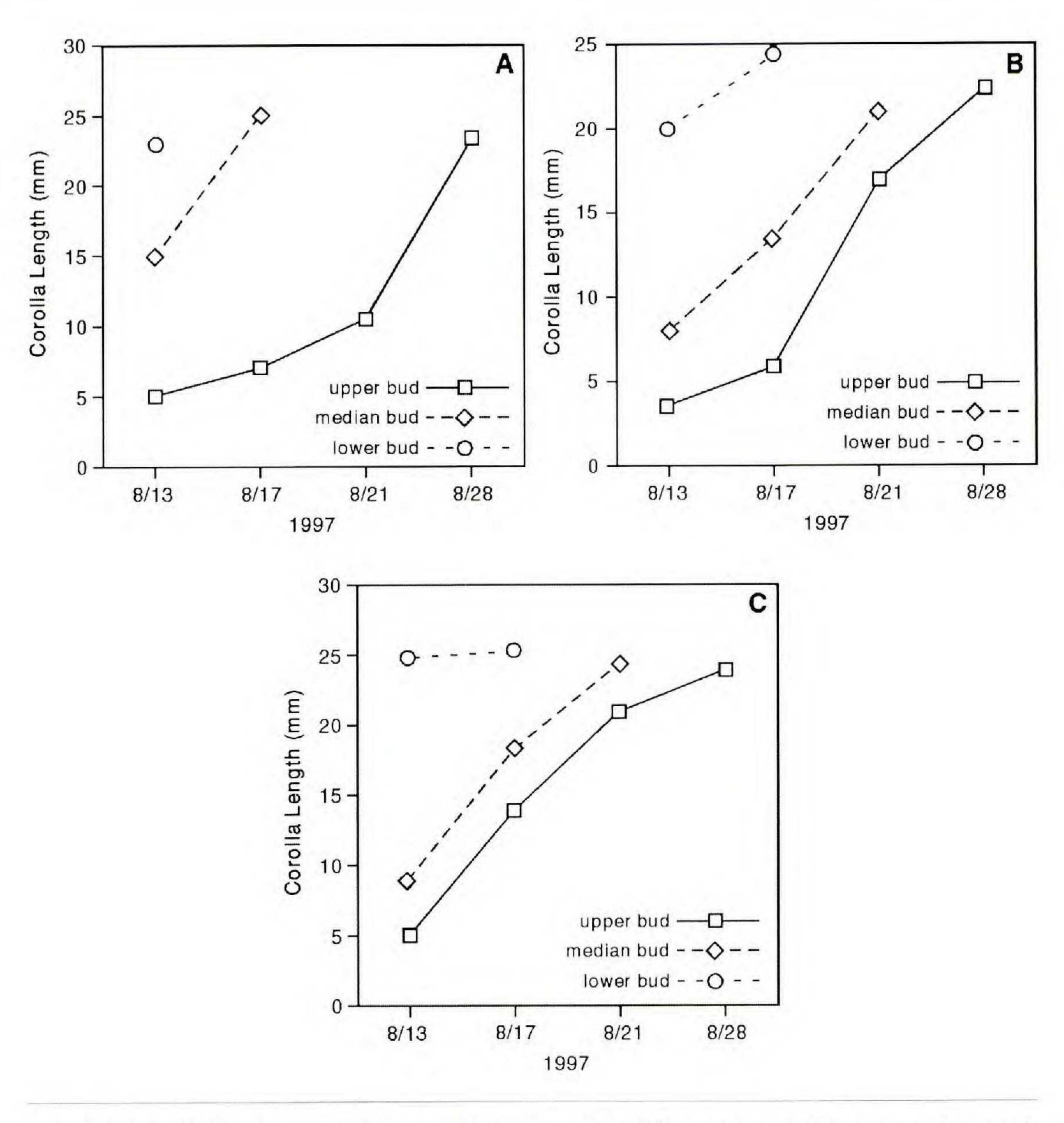


Fig. 4. Changes in corolla lengths from different positions on plant 59 at GWD during August 1997. A, terminal raceme; B, upper axillary raceme; C, lower axillary raceme.

calyx growth on the upper bud exhibited rapid elongation before reaching a plateau. Calyces of buds on the upper and lower axillary racemes (Fig. 5, b-c) also demonstrated rapid expansion before leveling off. The calyces of the upper buds were much shorter than those of the median and lower buds for all racemes examined.

Figure 6 illustrates calyx growth for the upper buds of the three racemes for three of the plants comprising the sample population. It shows that the upper axillary raceme had shorter calyces than did the lower axillary and terminal racemes for plants of the sample population.

Pedicels exhibited the same growth pattern as calyces. Bracts generally did not expand further once anthesis had occurred for an individual bud. Bracts

Table 3. Means and standard deviations for selected features of Macranthera flammea.

Character	Herbarium specimens		GWDp	GWD plants		
	X	S	N	X	S	N
calyx length, mm	10.89	3.51	254	18.44	4.28	27
corolla tube length, mm	21.10	1.24	263	22.78	2.49	9
corolla lobe length, mm	3.86	0.81	240			
corolla width, mm	4.71	0.78	194	4.11	0.43	9
fruit length, mm	11.22	1.81	102	10.61	0.64	12
fruit width, mm	9.0	1.41	102	8.7	0.52	12
pedicel length, mm	15.88	3.64	220	21.88	2.27	27
bract length, mm	21.38	14.31	133	32.15	9.47	27
upper leaf length, cm	5.59	1.53	93	9.59	1.47	12
upper leaf width, cm	1.8	0.9	93	3.19	0.77	12
lower leaf length, cm	12.5	3.81	28	19.72	2.03	12
lower leaf width, cm	4.21	2.26	28	4.03	0.41	12

did exhibit very rapid growth during bud expansion, and some of the bract lengths reached 50 mm for lower buds.

To produce more valid assessment of the amount of variation in calyx and corolla tube lengths observed in the GWD population (Table 3), we selected buds at various positions within the inflorescence and did not standardize to stage of development. The mean lengths of calyx, corolla, pedicel, and bract were greater in the GWD sample population because lower buds were included. Fruits measured in the GWD population tended to be shorter, narrower, and less variable than those in the herbarium specimens.

In general, variation was minimal in length and width of the corolla (Table 3, Fig. 4). Recent publications (Campbell et al. 1996; Smith et al. 1996; Temeles 1996) suggest that corolla width is the floral character selectively influenced by hummingbirds, a major pollinator of *M. flammea* (Pickens 1927).

The position of a flower within the framework of the inflorescence reflects its age (Harper 1977). Calyx length is determined by the position of a flower within the framework and is therefore determined by age of the flower. Observations (Figs. 5, 6) indicate calyces reach a plateau in their growth and do not continue to grow after flowering begins.

Pennell (1913) was correct in stating that the differences in the lengths of calyx lobes are due to the age of flowers. However, because lobes do not grow after anthesis, the position of the flower unit within the architecture of the inflorescence accounts for observed differences in calyx lengths. These growth characteristics are typical for plants with indeterminate inflorescences. Sepals, bracts, and pedicels are shorter for bud units at the tip of the raceme and longer for those near the bottom. Internodes at the tip of the raceme are truncated, those at the bottom elongated. Differences in the upper axillary branching po-

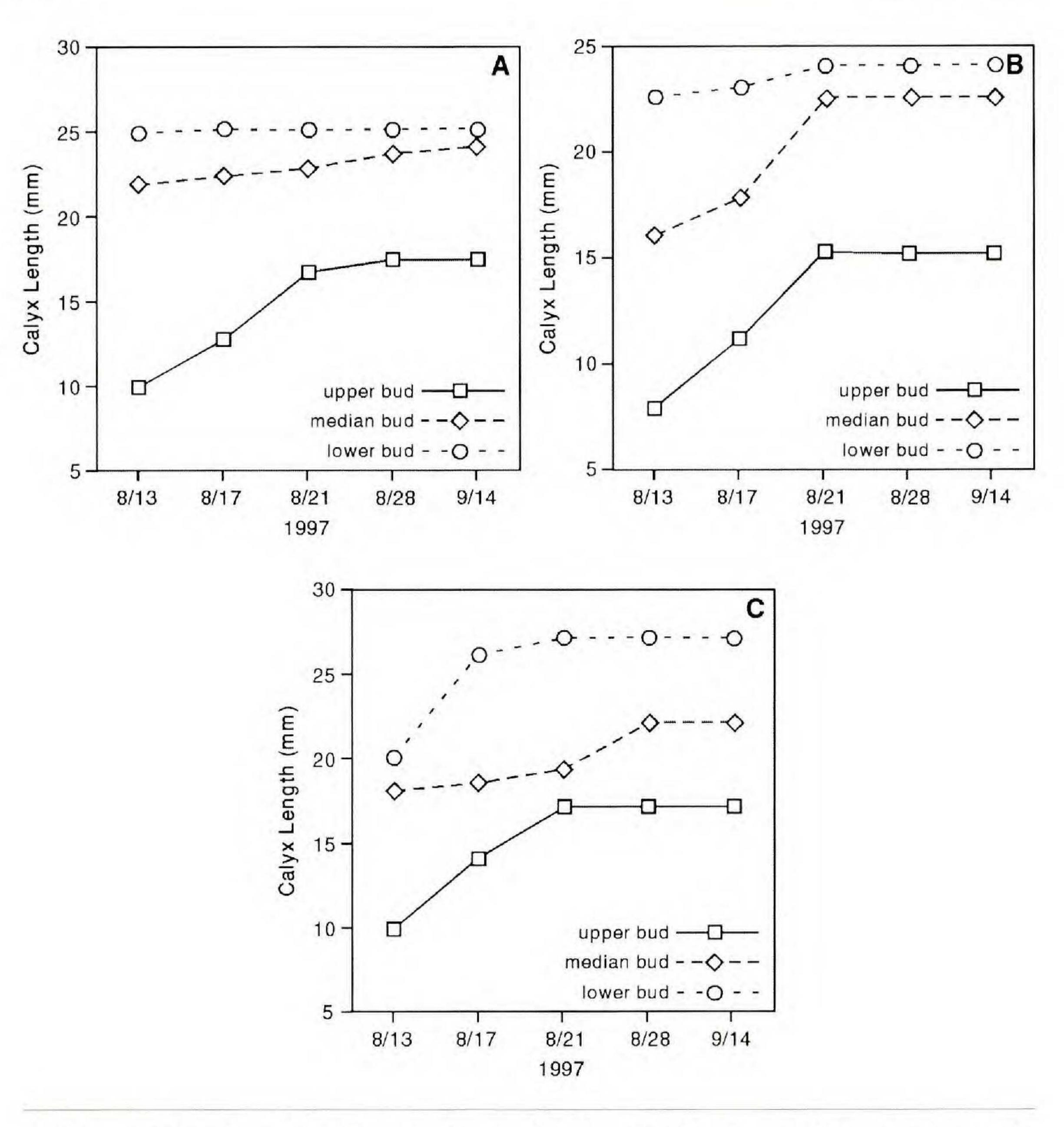


Fig. 5. Changes in calyx lengths from different positions on plant 59 at GWD during August 1997. A, terminal raceme; B, upper axillary raceme; C, lower axillary raceme.

sitions can be attributed to apical dominance. The terminal racemes are always the first to flower, followed closely by the lower axillary racemes. The racemes flower upwards on the inflorescence so that the upper axillary racemes are the last to reach anthesis (Fig. 2).

In general, as much variation appears to occur within a single plant or population as throughout the entire range. Observed variation in the characters of calyx, pedicel, and bract length can all be attributed to position effects within the architecture of the plant. Age determines the placement of individual flower units within an expanding inflorescence and therefore influences character morphology.

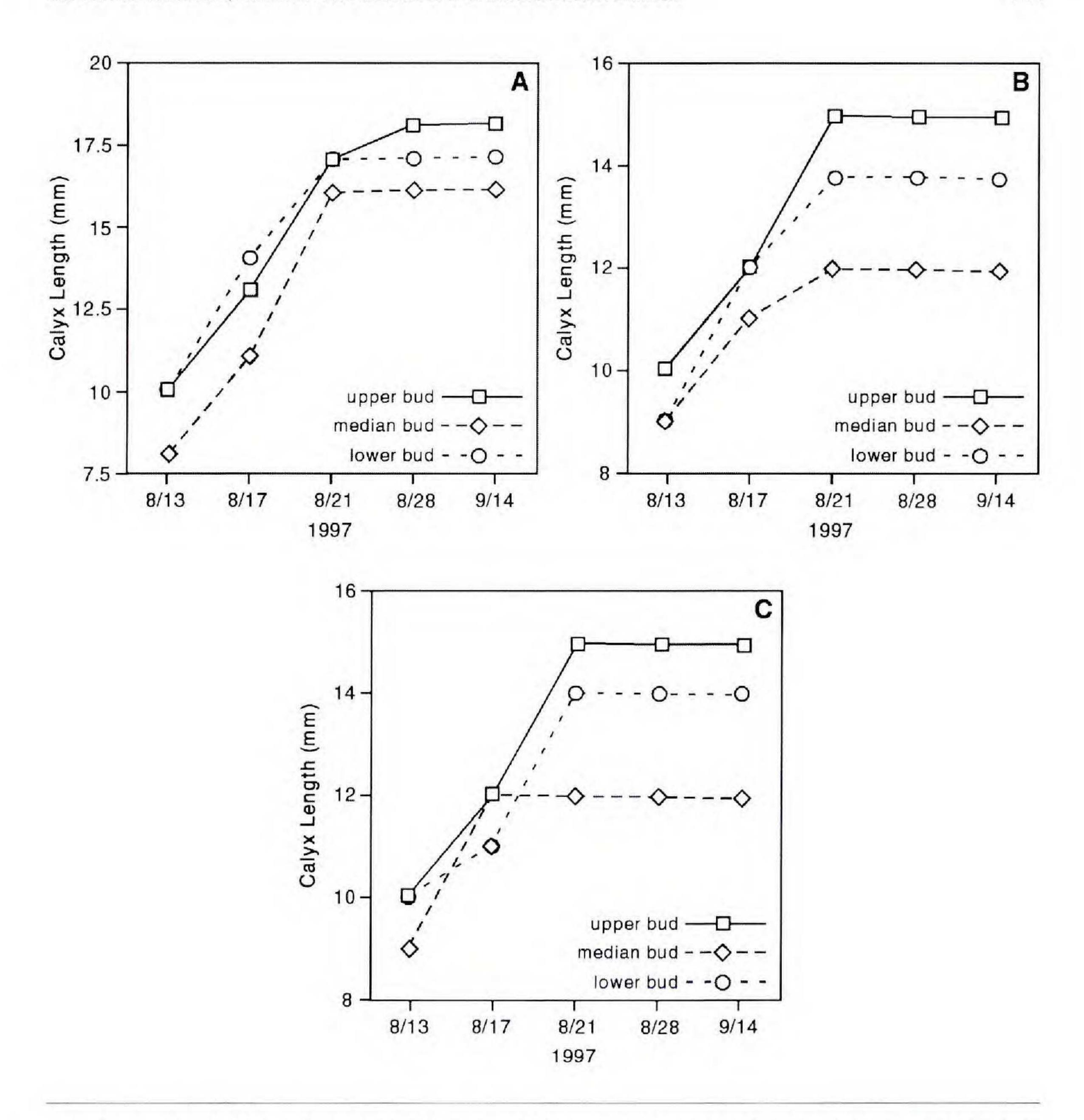


Fig. 6. Changes in calyx lengths from different positions on three separate plants at GWD during August 1997. A, terminal raceme; B, upper axillary raceme; C, lower axillary raceme.

Observations of herbarium specimens and the GWD population do not yield sufficient evidence of distinct variation in any character to warrant recognition of subspecific categories in *M. flammea*.

APPENDIX 1

Specimens examined and annotated documenting known range and morphological variability of *Macranthera flammea* (exact localities omitted because of species' rareness).

ALABAMA. Baldwin Co.: 7 Sep 1912, F.W. Pennell 4553 (US, PH); 15 Oct 1940, M.G. Henry 2445 (GA); 20 Aug 1947, M.G. Henry 4935a (PH); 23 Aug 1947, M.G. Henry 4942 (PH); 16 Sep 1964, S.M. McDaniel 5314 (FSU); 11 Sep 1979, W.S. Judd 2288 (FLAS); 20 Aug 1981, R. Kral 67854 (VDB). **Butler Co.:** 11 Oct

1970, *R. Kral* 41623 (VDB). **Conecuh Co.**: 21 Aug 1981, *R. Kral* 67829 (VDB); 18 Sep 1993, *R. Kral* 83317 (VDB). **Covington Co.**: 3 Sep 1985, *S.A. Thompson* 3011 (VSU). **Escambia Co.**: 21 Oct 1961, *R. Kral* 38617 (VDB, NY); 17 Aug 1978, *R. Kral* 32463 (VDB). **Geneva Co.**: 3 Sep 1969, *R. Kral* 36844 (VDB). **Mobile Co.**: 1872, *D.C. Mohr* (NY); 1878, *D.C. Mohr* (US, NY); Aug 1892, *D.C. Mohr* (NY); 16 Sep 1892, *D.C. Mohr* (US); 30 Aug 1912, *F.W. Pennell* 4406 (MO, US, PH); 31 Aug 1912, *F.W. Pennell* 4459 (PH); 31 Aug 1912, *F.W. Pennell* 4462 (PH); 4 Sep 1912, *F.W. Pennell* 4534 (MO, NY, PH); Jul 1919, *E.W. Graves* 1310 (MO); Aug 1919, *E.W. Graves* (US); 3 Sep 1966, *M.G. Lelong* 4041 (USAM); 26 Aug 1969, *H.D. Moore* 621 (VDB); 3 Sep 1972, *M.G. Lelong* 6800 (USAM, VDB). **Washington Co.**: 21 Sep 1969, *R. Kral* 37233 (FSU); 3 Sep 1970, *R. Kral* 41062 (JSU, VDB); 9 Sep 1970, *H.D. Moore* 1005 (VDB). **County unknown**: *Gates* (NY); *A. Gray* (GH); J.H. *Redfield* (MO).

FLORIDA. Bay Co.: 30 Oct 1957, M.G. Henry 6753 (PH); 3 Sep 1958, R.K. Godfrey 57619 (FSU). Calhoun Co.: 6 Sep 1964, R.K. Godfrey 64605 (FSU); 18 Sep 1964, S.M. McDaniel 5230 (FSU, VDB). Escambia Co.: 8 Aug 1955, E.S. Ford 4314 (FLAS); 21 Jul 1956, P.L. Redfearn & R. Kral 2727 FSU); 9 Sep 1980, J.R. Burkhalter (FLAS); 11 Sep 1982, J.R. Burkhalter 8470 (MO). Franklin Co.: 20 Sep 1912, F.W. Pennell 4681 (GH, NY, PH); 22 Sep 1968, A.K. Gholson 3133 (AKG); 7 Sep 1970, A.K. Gholson (AKG); 1 Sep 1976, L. Conde (FLAS); 12 Sep 1984, L. C. Anderson 7573 (FSU); 11 Sep 1985, L.C. Anderson 8798 (FSU). Gadsden Co.: Sep 1835, Chapman (NY, US); 1836, Chapman (GH); 10 Jan 1909, Chapman (GH); 30 Aug 1936, H. Foster 120 (FLAS). Holmes Co.: 3 Sep 1942, L.T. Nieland (FLAS); 27 Aug 1947, M.G. Henry 4967 (PH). Jackson Co.: 21 Aug 1971, L.J. Musselmann & G.S. Waggonner 4393 (FSU, GH, NY, ODU, GA, VDB); 10 Oct 1978, A.K. Gholson 7416 (AKG); 5 Oct 1979, A.K. Gholson 8004 (AKG); 11 Sep. 1983, A.K. Gholson 10629 (AKG). Leon Co.: 17 Sep 1960, H.L. Stripling 904 (FSU, 4 plants); 2 Jun 1970, R.J. Nielsson (FLAS). Liberty Co.: 3 Sep 1955, R.F. Thorne & R.A. Davidson 16831 (FLAS, FSU, GA); 11 Sep 1974, L.C. Anderson 3817 (FSU); 15 Sep 1979, R.K. Godfrey 77250 (FSU); 15 Sep 1979, A.K. Gholson 7985 (AKG); 7 Nov 1987, P.W. Alcorn 378 (FLAS); 13 Sep 1989, S.L. Orzell & E.L. Bridges 12054 (GA); 22 Oct 1993, L.C. Anderson 14594 (FSU); 13 Sep 1997, N. Jordan 16 (FSU); 27 Sep 1995, J.D. Alford 220 (FSU); 29 Sep 1997, J.D. Alford 1064 (FSU). Okaloosa Co.: 3 Oct 1949, S.C. Hood 3214 (FLAS); 19 Oct 1971, R.K. Godfrey 71005 (FSU); 2 Sep 1976, A.K. Gholson 7985 (AKG); 2 Sep 1976, R.K. Godfrey 75446(FSU); 16 Sep 1993, L.C. Anderson 14558 (FSU). Santa Rosa Co.: 9 Sep 1912, F.W. Pennell 4564 (MO, PH); 10 Sep 1912, F.W. Pennell 4595 (GA, PH, US); 25 Aug 1957, E.S. Ford 5403 (FLAS); 1 Nov 1969, S.M. McDaniel 12519 (FSU, VDB); 2 Sep 1976, R.K. Godfrey 75445 (FSU); 29 Sep 1990, J.R. Burkhalter 23487 (FSU). Walton Co.: 2 Oct 1901, A.H. Curtiss 6922 (GA, GH, MO, NY, US); 23 Sep 1956, R.K. Godfrey & R. Kral 55157 (FSU, GA); 25 Aug 1966, D.B. Ward 6006 (FLAS); 1 Oct 1970, H.A. Davis 15418 (FLAS, GA, VDB); 6 Sep 1972, E.H. Sargent & H.A. Davis 16029 (MO). County unknown: Chapman (NY); Mohr (NY).

GEORGIA. Bulloch Co.: H. Hall (GA). Crisp Co.: 4 Sep 1954, W. H. Duncan 18189 (GA, VSC). Early Co.: 12 Aug 1947, R.F. Thorne (GH, US); 25 Aug 1948, R.E. Thorne & W.C. Muenscher 8591 (GA). Emmanuel Co.: 2 Sep 1968, J.R. Bozeman 11727 (FSU, GA, GH, HATT, MISS, MO, NY, ODU, VDB, VSC); 22 Aug 1983, S.B. Jones 23813 (FSU, GA). Thomas Co.: 1897, S.M. Tracy (MO); 12 Sep 1998, J.D. Alford 1077 (FSU). Turner Co.: 21 Sep 1975, W.R. Faircloth 7893 (VSC). Ware Co.: 25 Aug 1946, F.S. Sargent 122 (US). Wilcox Co.: 28 Aug 1964, R. Kral 22278 (VDB). Worth Co.: 25 Aug 1947, R.F. Thorne 6362 (NY). County unknown: J.H. Redfield 12395 (MO).

LOUISIANA. St. Tammany Parish: 1846, Chapman (GH); 1846, Drummond (GH); 1909, A. Gray (GH); 11 Sep 1983, C.M. Allen 12911 (LSU); 7 Sep 1985, A.W. Lievens 1003 (LSU); 7 Sep 1985, L.E. Urbatsch (LSU). Washington Parish: 27 Sep 1936, C.A. Brown 6737 (LSU); 9 Sep 1962, C.A. Brown 17584 (LSU); 31 Aug 1967, L.J. Mussellmann 1243 (MO); 28 Oct 1967, J.W. Thieret 28304 (FSU, GH); 16 Aug 1970, D. Ziegler (MO); 13 Sep 1975, R.D. Thomas 46210 (VDB); 22 Oct 1975, Rich 209 (ODU); 20 Aug 1987, N.M. Gilmore 3288 (LSU).

MISSISSIPPI. Forrest Co.: 14 Aug 1947, M.G. Henry 4888 (PH); 7 Sep 1965, J.W. Carter 941 (HATT); 3 Oct 1970, K.E. Rogers 4679 (VDB); 15 Sep 1974, J.W. Wooten 2519 (USM); 24 July 1976, J.A. Barnes 648 (VDB). **George Co.**: 30 Sep 1995, S.W. Leonard 9173 (FSU, 26 plants). **Hancock Co.**: 17 Aug 1969, F.H.

Sargent 9885 (MO, VDB); 16 Sep 1970, S. B. Jones 20312 (FSU, GA, MISS, VDB); 16 Sep 1970, F.H. Sargent 10390 (FSU); 28 Aug 1972, H.L. Clark & K. Clark (FSU, HATT); 29 Aug 1977, M. Brooks (FSU). Harrison Co.: 16 Sep 1885, J.H. Redfield & J.D. Smith 16217 (GH, MO, NY, US); 18 July 1950, G.L. Webster & R.L. Wilbur 3460 (GH, NY, US); 18 Aug 1950, D. Demaree (VDB); 16 Aug 1952, D. Demaree 32853 (GH); 19 Aug 1971, C.A. Brown 22040 (LSU, NY). Jackson Co.: 11 Sep 1889, F.S. Earle (NY); 16 Aug 1947, M.G. Henry 4921 (PH); 18 Aug 1949, D. Demaree 28202 (NY); 20 Aug 1949, D. Demaree 28300 (NY, VDB); 24 Aug 1951, D. Demaree 31281 (VDB); 17 August 1952, R.L. Diener 509 (MO); 24 Aug 1953, R.B. Channell 343 (VDB); 11 Sep 1975, M. Arguelles 1455 (VSC). Lamar Co.: 14 Aug 1927, F. Cook (US). Layton Co.: 15 Aug 1925, F. Cook (US). Marion Co.: 8 Aug 1955, J.D. Ray (GA, GH, NY); 5 Sep 1963, R. Kral 19389 (VDB). Pearl River Co.: 19 Sep 1982, S.M. McDaniel 26507 (FSU). Perry Co.: 15 Aug 1947, M.G. Henry 4904 (PH); 4 Oct 1995, S.W. Leonard 9181 (FSU, 28 plants). Stone Co.: 24 Aug 1953, D. Demaree 34081 (GH, VDB); 8 Oct 1966, T.M. Pullen 661140 (UM). Winston Co.: 6 Sep 1932, F.H. Sargent (NY). County unknown: 30 Aug 1941, G.A. Girhart 87 (NY).

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